A REVIEW OF THE VERTEBRATE FAUNA OF THE LOWER JURASSIC NAVAJO SANDSTONE IN ARIZONA

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ABSTRACT

The Lower Jurassic Navajo Sandstone of northern Arizona and southern Utah has yielded a diverse assemblage of late Early Jurassic terrestrial tetrapods from eolian and associated paleoenvironments. Although rare, vertebrate body fossils are represented by specimens of tritylodonts, crocodylomorphs, sauropodomorphs, and basal theropods (including *Segisaurus halli*). The vertebrate ichnofossil record is diverse and includes synapsids (*Brasilichnium*), crocodylomorphs (cf. *Batrachopus*), ornithischians (*Anomoepus*), sauropodomorphs (*Navahopus* and *Otozoum*), theropods (*Grallator*, *Anchisauripus*, and *Eubrontes*), and several problematic morphs ("pterosaur", "lacertilian", and *Trisauropodiscus*). There is a high degree of concordance between the clades represented by the body fossils and ichnofossils. Taken together, they represent a typical Early Jurassic assemblage that is similar to other North American and foreign Early Jurassic terrestrial tetrapod assemblages, although a few forms are unique to the Navajo Sandstone (*Segisaurus* and *Navahopus*). The terminal Early Jurassic record of the Navajo Sandstone vertebrate assemblage suggests that little faunal change occurred through the course of the Early Jurassic Period in North America.

INTRODUCTION

THE LOWER Jurassic sediments of the Colorado Plateau represent one of the best terrestrial sediment records of this time anywhere within the world. These sediments encapsulate a critical time in the Early Mesozoic during a period of faunal turnover and intense climate change. Dinosaurs, crocodylomorphs, lepidosaurs, and lissamphibians were diversifying after extensive extinctions of tetrapods during the Late Triassic (Padian, 1986). At the same time, the Early Jurassic represents the last widespread appearance of non-mammaliaform synapsids such as tritylodonts (Sues, 1986).

The Navajo Sandstone is widespread throughout much of northern Arizona and southern Utah (Fig. 1). As part of the Glen Canyon Group (Harshbarger et al., 1957), this unit represents the terminal record of the Lower Jurassic in the southwestern United States (Clark and Fastovsky, 1986; Winkler et al., 1991) that was part of a continuous "sand sea" that covered much of the western margin of North America (Blakey, 1994). Its vertebrate fauna is important for several reasons. First, this is the only record of a late Early Jurassic vertebrate fauna in North America and one of the only records of this time worldwide (Winkler et al., 1991). Second, the Navajo vertebrate fauna samples a unique arid desert fauna not represented by other coeval sediments of the Glen Canyon Group.

Unfortunately, despite the importance of the Navajo record, very little paleontological research has concentrated on this formation. Isolated field investigations by the University of California Museum of Paleontology (Hall, 1934; Camp, 1936) and Major L.F. Brady of the Museum of Northern Arizona (Brady, 1935; 1936; Baird, 1980) discovered isolated but intriguing dinosaur body fossil remains. More recently, fieldwork by D.A. Winkler (1991) and others has discovered additional vertebrate material, though most recent work in the Navajo Sandstone has concentrated on the abundant vertebrate ichnological record preserved in the strata (e.g., Rainforth, 1997; Lockley et al., 1998).

Institutional Abbreviations. — MNA, Museum of Northern Arizona, Flagstaff, AZ; NMMNH, New Mexico Museum of Natural History, Albuquerque, New Mexico; SMU, Southern Methodist University, Dallas, Texas; UCMP, University of California Museum of Paleontology, Berkeley, CA.

GEOLOGIC SETTING

The Navajo Sandstone is the uppermost unit of the Glen Canyon Group (Harshbarger et al., 1957). The Glen Canyon Group is a set of fluvial and eolian terrestrial sediments that is Early Jurassic in age (Olsen and Galton, 1977; Clark and Fastovsky, 1986), although the base of the group may be Late Triassic in age (Morales and Ash, 1993). The group is divided into formations primarily based upon depositional environment (fluvial-lacustrine vs. eolian) because nearly all units have gradational

contacts with each other (Blakey, 1994). The base of the Navajo Sandstone is a gradational contact with the Kayenta Formation, composed of complex intertongues that begin over 100 meters below the main body of the Navajo Sandstone (Middleton and Blakey, 1983). This contact reflects a transition from the braided and meandering stream siltstones and sandstones of the Kayenta Formation to the massively crossbedded eolian sandstones of the Navajo Formation (Middleton and Blakey, 1983). The deposition of the Navajo system represents the advancement of a large desert "sand sea" over the arid fluvial environment of the partly underlying Kayenta stream system (Blakey, 1994). The formation thickens gradually to the west with the thickest section found in southeast Utah (Blakey, 1994). Based on palynomorph assemblages from the underlying Moenave Formation, the Navajo Sandstone is probably no earlier than Pliensbachian in age (Litwin, 1986). The vertebrate assemblages in the Navajo Sandstone, as well as the partially laterally equivalent Kayenta Formation, show that these units are Early Jurassic in age (Olsen and Galton, 1977; Sues, 1985; Clark and Fastovsky, 1986).

Much of the Jurassic sediments of western North America were deposited in a large north-south retroarc basin directly to the east of highlands related to subduction on the western margin of North America (Kocurek and Dott, 1983). These sediments comprise a thick sequence of eolian and fluvial sediments in the east that grade into shallow marine sediments in the west (Kocurek and Dott, 1983; Blakey, 1994). The source for these sediments is generally inferred to be from exposed upper Paleozoic and Triassic rocks in Montana and Wyoming, including minor input from other eastern and southeastern sources (Kocurek and Dott, 1983).

During this time, the southwestern United States was located in the tropics, around 9º latitude (Loope et al., 2004a). As a result, strong modified trade winds blew from the northwest and drove a conveyor-belt system of sand deposition from north to south (Kocurek and Dott, 1983; Loope et al., 2004a). This interpretation is borne out by consistent paleocurrent data derived from the Navajo and other Jurassic eolian formations (Kocurek and Dott, 1983; Blakey, 1994). The global climate at this time was already warm and arid (Kocurek and Dott, 1983; Blakey, 1994), and this climate regime is evident in the Navajo Sandstone as well. The transition from the fluvial sediments of the Kayenta Formation to the eolian sands of the Navajo Sandstone indicates in part increasing aridity (Middleton and Blakey, 1983; Blakey, 1994), and within the Navajo itself there is a relative transition from wetter to drier sediments as

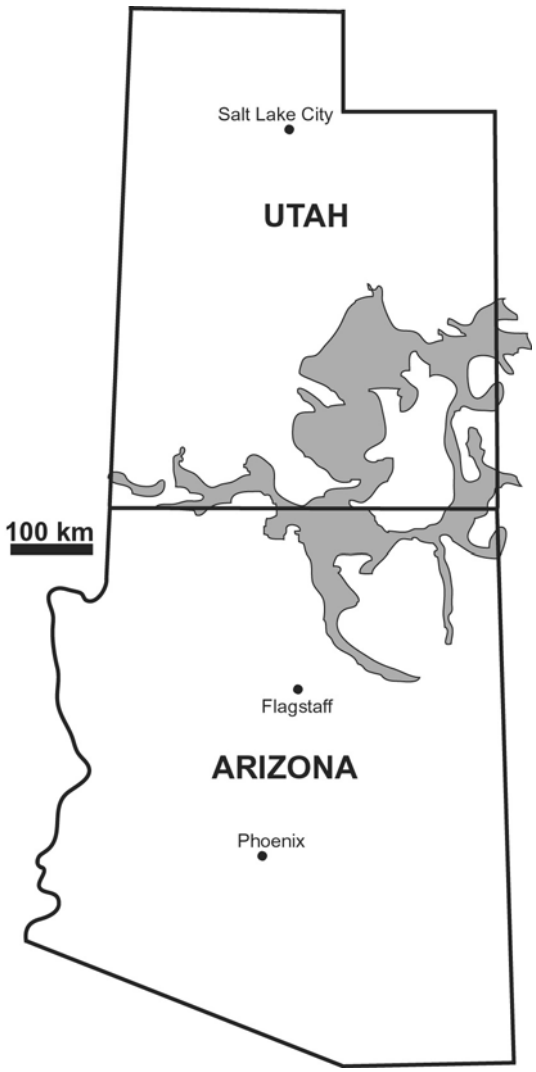

FIGURE 1. Distribution of exposed Navajo Sandstone strata in Arizona and Utah. Modified from Winkler et al. (1991).

one goes stratigraphically up section (Blakey, 1994; Loope and Rowe, 2003). Loope and Rowe (2003) identified several occurrences of sustained pluvial environments in the Navajo Sandstone with extremely wet interdunes developed between the migrating dunes. Common slumps in the dune faces also appear to be evidence for an arid monsoon model of precipitation for the early Mesozoic of Pangaea (Loope et al., 2001).

Most sediments within the Navajo Sandstone are large dune foresets of quartz-rich sandstone with large-scale planar-tabular crossbedding. However, interspersed within these dunes are restricted interdune settings (Winkler et al., 1991; Eisenberg, 2003). These lower boundaries between the interdune and dune commonly consist of a 1st-order bounding surface with root casts and mud

cracks (Winkler et al., 1991). The interdune itself can consist of a variety of lithologies including planar-bedded mudstone and sandstone, and dolomitic limestone, and are often disrupted by bioturbation (Eisenberg, 2003). "Stromatolites" (i.e., cryptalgal laminations in carbonates) can also be present, and often reach large sizes (Middleton and Blakey, 1983; Eisenberg, 2003). The presence of these biogenic structures suggests a steady water supply for the interdune, at least while the stromatolites were growing (Eisenberg, 2003). In some cases, the stromatolites are overlain by mass-flow sequences containing breccias of rip-up carbonate clasts from the underlying interdune sediments (Eisenberg, 2003). These examples of flood deposits reinforce the interpretation that large quantities of water sometimes inundated the Navajo eolian system (Loope et al., 2004b).

A variety of non-vertebrate fossils have been described from the Navajo Sandstone, many in association with interdune deposits. Besides the stromatolites described above, root casts, horsetails ("*Equisitum*" sp.), and ostracodes are also known from the interdune sediments, especially the limestones (Harshbarger et al., 1957; Winkler et al., 1991). Locally common specimens of *in situ* permineralized wood are known from interdune deposits in southern Utah, further supporting the presence of a stable water source in these environments (Stokes, 1991; Loope et al., 2004b). Abundant insect trace fossils are known from clastic interdune and associated dune deposits (Loope and Rowe, 2003).

BODY FOSSILS

Tritylodontidae.—Winkler et al. (1991) described a single tritylodont specimen (SMU 70527) from northern Arizona. This specimen is partially articulated and preserves most of the trunk skeleton including the pectoral girdle, forelimbs, dorsal vertebrae, pelvic girdle, and partial hindlimbs. Winkler et al. (1991) tentatively allied the specimen with *Kayentatherium* based on the presence of transverse expansions of the dorsal vertebral neural arches on the dorsal vertebrae. However, Sues et al. (1994) considered the specimen non-diagnostic and referred it to Tritylodontidae indet.

The presence of a robust olecranon process on the ulna of the tritylodont was interpreted as evidence for adaptation to scratch-digging (Winkler et al., 1991), and fossorial adaptations in tritylodonts were also proposed by Sues (1984). Although enlargement of the olecranon process is common in scratch-diggers, it is not unique to this mode of life, and simply implies a potential increase of force for movement of the forelimb. Considering the arid Navajo environment, a fossorial or digging lifestyle is a possibility, but such an interpretation requires a comprehensive biomechanical analysis of the skeleton.

SMU 70527 was preserved at the boundary between a bioturbated fine/very fine sandstone and an overlying mudstone, and these sediments were overlain by limey sandstone (Winkler et al., 1991). The combination of these facies is diagnostic of interdune deposits in the Navajo Sandstone (Eisenberg, 2003), and confirms Winkler et al.'s (1991) interpretation that the specimen was preserved in a wet interdune.

Crocodylomorpha.—Three crocodylomorph specimens have been reported from the Navajo Sandstone of northern Arizona. All specimens have been referred to the Protosuchidae, a group that as traditionally defined is probably paraphyletic, although the described Early Jurassic North American species are all included in a monophyletic clade (Pol and Norell, 2004; see Wu et al., 1997 for an alternate view of protosuchian monophyly). This referral is based mainly on the morphology of the preserved armor and the fact that the fossils are Early Jurassic in age (Rinehart et al., 2001).

UCMP 61229 consists of two articulated series of osteoderms and isolated pes (Fig. 2). One sequence of osteoderms from the caudal region is exposed in ventral view and most of the bone is eroded away, with the right side missing (Fig. 2A,B). The first three preserved osteoderms of the other series are nearly complete and have been prepared from the opposite side (Fig. 2C). They possess light sculpturing and no lateral osteoderms are apparent. Galton (1971) interpreted them to be from the cervical region based on comparison with *Protosuchus*. The right pes is nearly complete, except for some of the metatarsals, proximal phalanges and part of the astragalus that were eroded away (Fig. 2D,E).

Galton (1971) referred this specimen to *Protosuchus* sp. based on similarity with corresponding elements in *Protosuchus richardsoni* (Colbert and Mook, 1951). Unfortunately, UCMP 61229 possesses no discrete synapomorphies of *Protosuchus* and is therefore not diagnostic to this clade (Clark and Fastovsky, 1986; Sues et al., 1994). Although the transversely broadened dorsal osteoderms are characteristic of many crocodyliforms (e.g., Colbert and Mook, 1951), they are also found in some "sphenosuchians" outside this clade (Clark and Sues, 2002). Therefore, UCMP 61229 is referred to Crocodylomorpha indet.

Detailed locality and sedimentological data are not available for this specimen. The preserved

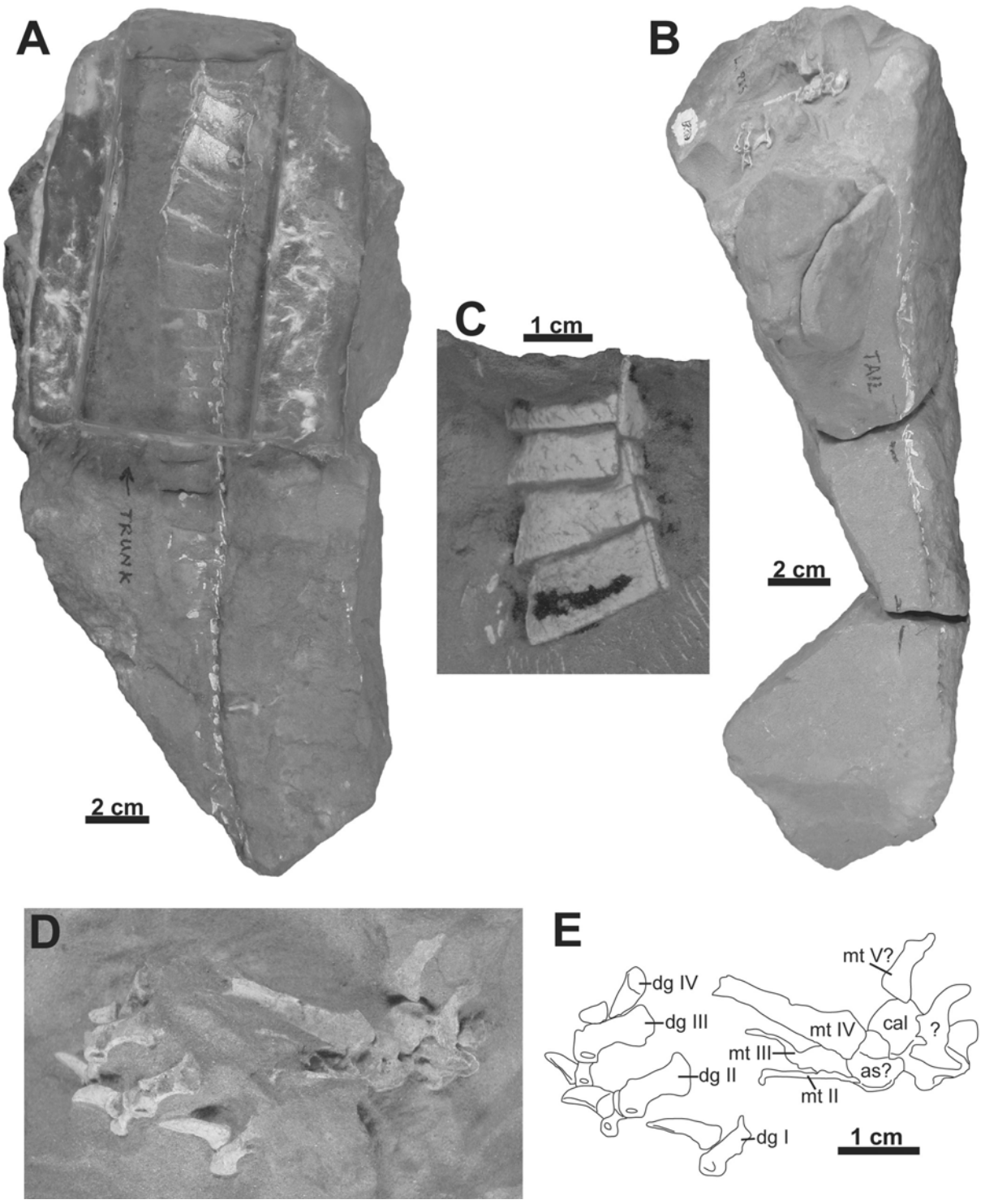

FIGURE 2. Partial skeleton of indeterminate crocodylomorph (UCMP 61229) from the Navajo Sandstone of northern Arizona. *A*, Posterior dorsal and proximal caudal osteoderms in ventral view. *B*, Distal caudal osteoderms in ?ventral view and right pes in oblique dorsal view. *C*, Posterior dorsal osteoderms in dorsal view. *D*, *E*, Articulated right pes in dorsal view. **Abbreviations**: **as**, astragalus; **cal**, calcaneum; **dg**, digit; **mt**, metatarsal; **?**, unknown.

matrix is a homogeneous quartz-arenite sandstone lacking any sedimentary structures. Petrographic examination of the sandstone in thin section reveals medium sorted very fine to fine sub-angular to sub-rounded frosted grains of monocrystalline quartz that are common in eolian sandstones. 1-2% of the grains are very fine angular lithic fragments. No cross-beds are apparent in the preserved matrix, so this specimen could be derived from an interdunal sandstone that has remobilized eolian sediment.

Rinehart et al. (2000, 2001) reported two crocodylomorph specimens from north-central Arizona near the Utah border. The first specimen, NMMNH P-33097, includes an articulated series of eroded dorsal centra, impressions of ribs and ventral osteoderms, isolated dorsal osteoderms, and a partial articulated pes. Again, this specimen was referred to a "protosuchid crocodylomorph" based on osteoderm and pes morphology consistent with *Protosuchus* and stratigraphic age (Rinehart et al., 2000; 2001). Like the UCMP specimen, the preserved material is only diagnostic to Crocodylomorpha indet. NMMNH P-33098 preserves an articulated partial manus, impressions of gastralia, a partial pes, and several isolated partial osteoderms. It is also referable to Crocodylomorpha indet.

The NMMNH specimens are derived from fine-grained sandstone containing rip-up clasts of mudstone and limestone (Rinehart et al., 2001). This unit is underlain by parent beds of the intraclasts (Rinehart et al., 2001) and probably represents a localized channel deposit within an interdune setting. It probably is not a mass flow deposit, as these are generally the terminal deposits of interdunes (Eisenberg, 2003), and the sandstone with the NMMNH specimens is overlain by planar-bedded sandstone of interdune origin (Rinehart et al., 2001).

Dinosauria indet.—Winkler et al. (1991) mentioned the presence of a small dinosaur tibia east of the locality of the SMU tritylodontid specimen. Unfortunately, the tibia was not collected, so its identification cannot be confirmed. It was found in a muddy sandstone that is part of an interdunal deposit (Winkler et al., 1991).

Sauropodomorpha.—Brady (1935, 1936) was the first to report sauropodomorph body fossils from the Navajo Sandstone of Arizona. Although he considered the specimen to be a "primitive theropod" following contemporary established taxonomic schemes, he recognized its close affinities to specimens described by Marsh as members of the Anchisauridae, which are now known to be sauropodomorphs (Yates, 2004). The specimen consists of both pedes (Fig. 3), a poorly preserved fragmentary pelvis, portions of articulated caudal vertebrae, and several articulated gastralia. It has been published in the literature as MNA G2 7233 (e.g., Galton, 1971; Yates, 2004), although the specimen is currently catalogued and labeled as MNA V743 through MNA V752. Nevertheless, it is clear from the original description and figures that this constitutes a single specimen (Brady, 1935).

Galton (1971) briefly described the specimen and referred it to *Ammosaurus* cf. *A. major* based on the similarity of the pes to the type material of *Ammosaurus major*. Galton (1976) reiterated his referral of the specimen to *Ammosaurus* and included additional descriptions and figures of the material. Yates (2004) recently revised *Anchisaurus* and *Ammosaurus*, and convincingly demonstrated that the two are synonymous. He further concluded that the MNA specimen represents an indeterminate sauropodomorph that does not display any synapomorphies of *Anchisaurus*. Characters of Yates's analysis (2004) present in the MNA material include proximal neural caudal spines greater than half the length of the neural arch (104), length of mid-caudal centra less than twice the height of their anterior faces (108), length of longest chevron greater than the length of the preceding centrum (110), and phalanges of pedal digit V present (204) (Fig. 3). Character 104 is an unambiguous synapomorphy of Sauropodomorpha *sensu lato* (everything closer to sauropods than to theropods), and characters 108 and 110 are unambiguous synapomorphies of the clade *Efraasia* + (Prosauropoda + Sauropoda) (Yates, 2004). Character 204 is also a synapomorphy of this clade under accelerated transformation. The coding for character 197 is equivocal because the proximal end of metatarsal V is slightly obscured by metatarsal IV (Fig. 3B); however, it appears to have state one. If this is correct, it would suggest that the MNA specimen is excluded from the clade Prosauropoda + Sauropoda. The lack of a robust pedal digit V excludes the specimen from the clade *Vulcanodon* + Eusauropoda (Yates, 2004) (Fig. 3). Therefore, it is clear that the MNA material represents an indeterminate basal sauropodomorph and cannot be referred to *Anchisaurus* (*=Ammosaurus*).

The specimen is preserved in orange to orange-red fine sandstone that does not display any sedimentary structures. Brady (1936) said the material was found in "typical cross-bedded Navajo Sandstone". Until the locality is relocated, it is reasonable to assume that the specimen was preserved in the foresets of a migrating dune deposit.

The second sauropodomorph specimen known from the Navajo Sandstone, UCMP 82961, was found in northern Arizona by M. Wetherill in 1938 (Galton, 1971). It was collected by Charles L. Camp and includes an articulated left manus, isolated material of the right manus, crushed forelimb

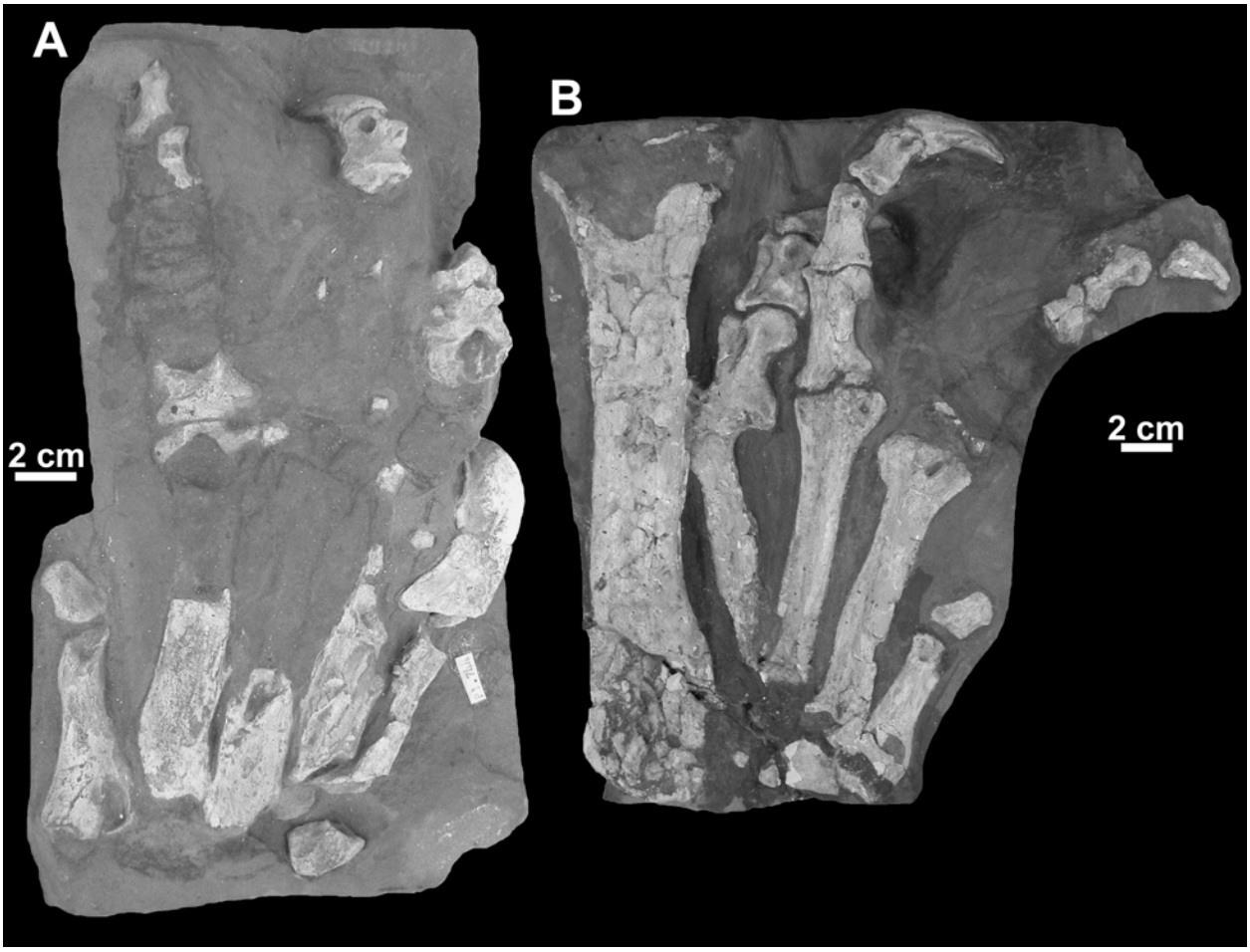

FIGURE 3. Pedes of MNA basal sauropodomorph specimen from the Navajo Sandstone of northern Arizona. *A*, Left pes (MNA V744) in dorsal view. *B*, Right tibia and pes (MNA V745) in dorsal view.

fragments, several cervical vertebrae and cervical ribs, and many additional fragments that were collected as float (Fig. 4). Galton (1976) considered these bone fragments to be uninformative, but Camp collected them in groups based on spatial distribution (Camp, unpublished 1938 field notes). Recent re-examination of the specimen by Tim Fedak (Dalhousie University) and the author suggests that at least some pieces fit together and may include pectoral girdle elements.

Galton (1971) first figured and described UCMP 82961. Like the MNA specimen, he referred it to *Ammosaurus* cf. *A. major* on the overall similarity of the manus to the type material of *Ammosaurus*. He later described and figured the material more extensively (Galton, 1976), reiterating his identification as *Ammosaurus*. Yates (2004) noted that UCMP 82961 possessed no synapomorphies of *Anchisaurus* (=*Ammosaurus*), and considered the material to represent a plateosaurian sauropodomorph on the basis of the enlarged distal carpal 1 that overlaps distal carpal 2, although this could be due to slight disarticulation of elements (Fig. 4A,B,C). He further suggested a possible relationship with *Massospondylus* based on the differences of ungual size among digits I, II, and III (Fig. 4A,B) (Yates, 2004).

The specimen is preserved in orange-red very fine to fine-grained sandstone. In thin section, it is identical to the matrix of crocodylomorph specimen UCMP 61229. The preserved matrix does not contain any sedimentary structures, and so it is possible that it came from either a dunal or interdunal deposit.

Theropoda.—A partial theropod skeleton discovered by the Rainbow Bridge-Monument Valley Expedition of 1933 in northern Arizona (Hall, 1934) was described by Camp (1936) as a new genus and species, *Segisaurus halli*. This partially articulated specimen consists of portions of the vertebral

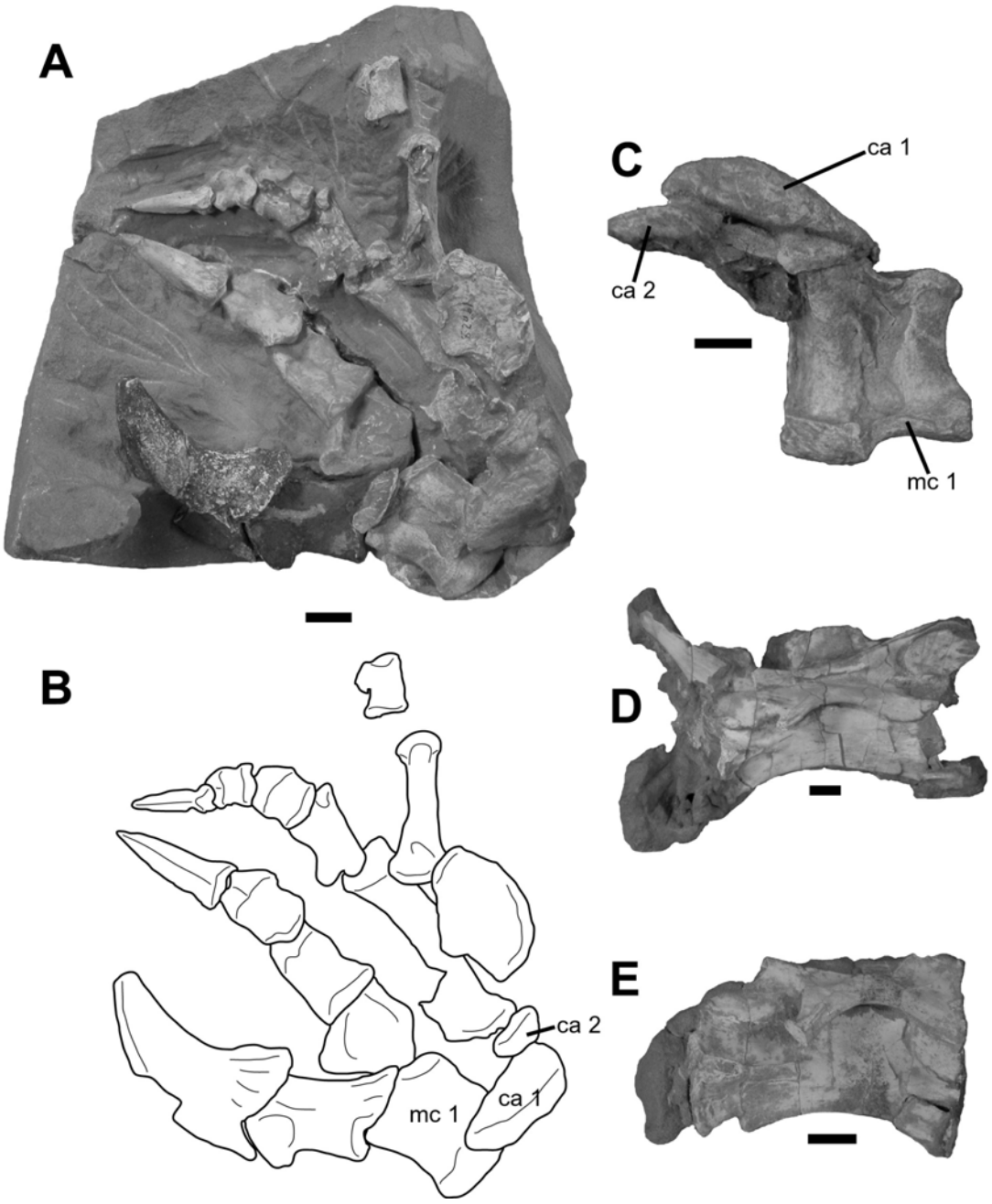

FIGURE 4. Selected elements of basal sauropodomorph specimen UCMP 82961 from the Navajo Sandstone of northern Arizona. *A*,*B*, Left manus in ventral view. *C*, Left distal carpals I and II, and metacarpal I in ventral view. *D*, *E*, Cervical vertebrae in left lateral view. **Abbreviations**: **ca 1**, distal carpal I; **ca 2**, distal carpal II; **mc 1**, metacarpal I. Scale bars equal 1 cm.

column, much of the forelimb, partial pelvis, most of the hindlimb, and many gastralia (Fig. 5). Camp recognized that *Segisaurus* was distinct from other small carnivorous dinosaurs known at the time (e.g., *Compsognathus* and *Ornitholestes*), and named a new family, the Segisauridae.

Gauthier (1986) was the first to consider *Segisaurus* a "ceratosaur", and Rowe and Gauthier (1990) were the first to explicitly consider it a coelophysoid theropod. Features of the pelvis and hindlimb such as the presence of a pubic fenestra (in addition to the obturator foramen) (Fig. 5A) (Rauhut, 2003) and a straight pubic shaft (Carrano et al., 2002)

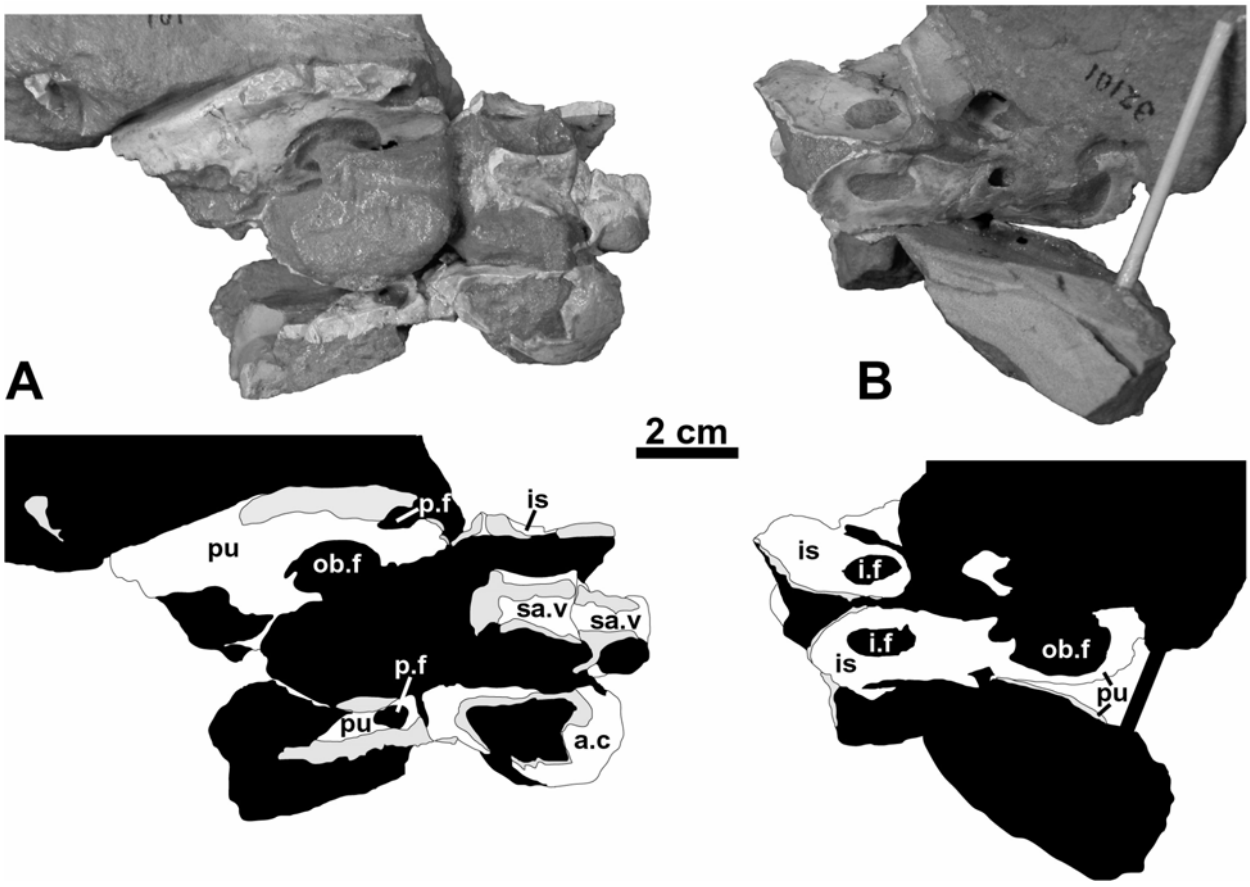

FIGURE 5. Pelvic block of the holotype (UCMP 32101) of *Segisaurus halli* from the Navajo Sandstone of northern Arizona. *A*, Pelvic block in dorsal view. *B*, Pelvic block in ventral view. White indicates original bone surface, grey indicates broken bone, and black is matrix. **Abbreviations**: **a.c**; supracetabular crest; **i.f.**, ischial fenestra; **is**, ischium; **ob.f**, obturator foramen; **p.f**, pubic fenestra; **pu**, pubis; **sa.v**, sacral vertebra.

confirm this assignment. Although much of the ischial shaft is not preserved, the additional coelophysoid character of an ischium equal in length to the pubis (Carrano et al., 2002) is likely based on the relative position of the blocks as illustrated by Camp (1936: pl. 3). A redescription of *Segisaurus* is forthcoming (Carrano et al., in press), so discussion of the specimen is limited here. A remarkable feature revealed by new preparation is the presence of a furcula (Senter and Hutchinson, 2001; Rauhut, 2003), rather than an unpaired clavicle as Camp (1936) described. Furculae have recently been described from other coelophysoids as well (Downs, 2000; Tykoski et al., 2002), suggesting that a furcula is plesiomorphic within Neotheropoda.

The depositional environment of *Segisaurus halli* is somewhat enigmatic. Camp (1936: p. 39-40) wrote:

"According to notes made by Mr. VanderHoof, the specimen lay on a tilted plane parallel to the planes of cross-bedding of the Navajo sandstone at that point (Fig 8). The axis of the body was horizontal and the right hind foot was pressed into the sand above the level of the left. Mixed with the red sandstone matrix in which the fossil is preserved are lumps of soft, dark maroon shale. These shaley lumps become more abundant a few feet above the level of the fossil, and ten feet above the specimen 'is a layer of exceedingly fine-grained limestone with enough flecks of carbonaceous material dispersed through it to give a greyish cast to the whole. It is probably a freshwater ... limestone and is here about three feet thick, though elsewhere quite thin in spite of its areal persistence in the Segi Canyon region.'"

The overlying strata he describes match the criteria for Navajo interdune deposits (Eisenberg, 2003), however, the sedimentology of the bed produced the specimen is unclear. The description implies it was preserved in the dune foresets because it was parallel to cross-bedding. The matrix does not support this

interpretation, because the red mudstone rip-up clasts do not suggest eolian deposition. These mudstone clasts range in size from 5 mm to 25 mm (although most are between 5 and 10 mm), are angular to subangular, and sometimes show some alignment. Unfortunately, the relation of this alignment to the original bedding is unknown. Existing matrix surrounding the specimen displays no other sedimentary structures. Petrographic analysis in thin section indicates that the sandstone matrix is composed of very fine to fine sub-angular to sub-rounded frosted monocrystalline quartz grains. As with the other sandstones examined under thin section, 1-2% of the grains are very fine angular lithic fragments. The mudstone clasts contain a few scattered sand grains, and the border between the clasts and the sandstone is generally distinct but not completely uniform. Altogether, this facies does not match that seen in mass flow deposits (Eisenberg, 2003), nor does it suggest failure of the dune face due to water saturation (e.g., Loope et al., 1999). The lithology may be evidence of an ephemeral fluvial channel that preserved *Segisaurus* (D. Loope, pers. comm.), although re-examination of the type locality is required to confirm this interpretation.

Winkler et al. (1991) reported finding a theropod tooth along with indeterminate bone fragments in a bioturbated sandstone. Examination of bone fragments associated with UCMP 61229 revealed a partial tooth (Fig. 6). Both of these specimens could represent either a theropod or large crocodylomorph.

Paleoenvironmental distribution of body fossils.—The rare remains of vertebrate body fossils described above can be placed in distinct paleoenvironments based on their individual depositional settings. Given such a low sample size, it would be unwise to use this data to suggest actual fauna segregation of the taxa. Only one specimen, the MNA sauropodomorph, can be reasonably assigned to dune facies. Two other specimens, the UCMP sauropodomorph and crocodylomorph, may also have been found in dune facies, but this cannot be confirmed without relocating the original localities. Both the tritylodontid and uncollected dinosaur specimen described by Winkler et al. (1991) are from interdune deposits. The two NMMNH crocodylomorph specimens as well as the holotype of *Segisaurus* may be from channel deposits associated with interdune deposits.

Although the body fossil record of the Navajo Sandstone is poor, the variety of depositional environments that preserve vertebrate fossils indicates that at least some of these animals probably inhabited both dune and interdune environments. Extensive post-mortem transport is unlikely, because most specimens are associated and often articulated. The distribution of known vertebrate fossils, although not statistically significant, seems to suggest that future prospecting of the Navajo Sandstone for vertebrate fossils should focus on interdune and related facies.

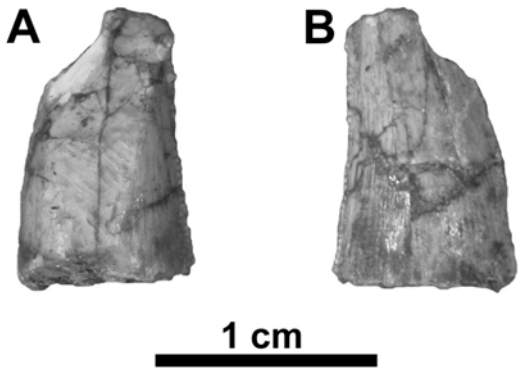

FIGURE 6. Partial isolated theropod or crocodylomorph tooth found with specimen UCMP 61229 from the Navajo Sandstone of northern Arizona.

ICHNOFOSSILS

The Navajo Sandstone contains a diverse assemblage of vertebrate footprints that contrasts with the meager amount of body fossil remains. Tracksites range from single footprints to trackways and highly trampled land surfaces (Loope and Rowe, 2003). Differences in faunal composition of tracks and underlying sedimentology at particular localities have led some workers to develop the "vertebrate ichnofacies" concept (Lockley et al., 1994). It suggests that certain depositional environments can be identified based on the taxic composition of vertebrate ichnofossils at a site. For example, in the Navajo Sandstone small footprints are found in dune foreset strata whereas larger taxa are found in planar-bedded interdune lithofacies (Rainforth, 2001a). Recent work in the Navajo Sandstone by Rainforth (1997, 2001a), however, suggests that the supposed segregation of footprint assemblages is a result of preservational bias, rather than particular vertebrates living in different environments. Rainforth (1997) suggested that the predominance of carnivorous track-makers was partially due to behavior preferences, but this inference is not directly testable.

For most of the history of vertebrate ichnology, track-makers have been identified based on overall similarity between the footprint and known vertebrate taxa from coeval sediments. This is the case for most of the Navajo Sandstone tracks. Only

recently have some workers started to use synapomorphy-based identifications for track-makers (Olsen et al., 1998; Carrano and Wilson, 2001; Padian, 2003). For example, *Grallator* and *Eubrontes* footprints in the Navajo Sandstone have been assigned to "ceratosaur" theropods (e.g., Lockley and Hunt, 1995; Rainforth, 1997), but based on our current understanding of the distribution of pes synapomorphies across the Dinosauria, they can only be weakly constrained to Theropoda based on apomorphic traits (Olsen et al., 1998). It is beyond the scope of this paper to critically re-examine proposed track-makers for every footprint morph in the Navajo Sandstone; however, the cautionary note above should be kept in mind.

Many of the following taxa have been studied predominantly in southern Utah, but it is reasonable to assume that the animals also inhabited the Arizona portion of the Navajo depositional basin.

Synapsida.—Tracks assigned to the ichnogenus *Brasilichnium* (Fig. 7A) are common throughout the Navajo Sandstone of Arizona and Utah (Lockley and Hunt, 1995; Rainforth, 1997). They are the most common vertebrate ichnofossil in dune foreset facies of the Navajo Sandstone (Rainforth, 1997). The pes print has a semi-circular posterior margin and is pentadactyl, with rarely preserved manus prints that have an ambiguous morphology (Rainforth, 1997). These tracks have been assigned variously to non-mammalian synapsids and mammaliaforms based on similarities with the pes of these taxa (Lockley and Hunt, 1995; Rainforth, 1997).

Crocodylomorpha. — Tracks of cf. *Batrachopus* (Fig. 7B) have been reported from southern Utah in the Navajo Sandstone (Lockley and Hunt, 1995; Rainforth, 1997). *Batrachopus* footprints have tetradactyl manus and pes prints and examples from the slightly older Moenave Formation of the Glen Canyon Group have been convincingly demonstrated to be from crocodylomorph archosaurs (Olsen and Padian, 1986).

?Pterosauria.—Stokes (1978; Stokes and Madsen, 1979) reported the presence of *Pteraichnus* trackways in the Navajo Sandstone of southern Utah. Regardless of the controversy surrounding the track-maker(s) of *Pteraichnus* (e.g., Padian and Olsen, 1984; Lockley et al., 1995; Mazin et al., 2003; Padian, 2003), all authors after Stokes agree that the Navajo tracks are not referable to *Pteraichnus* (Lockley and Hunt, 1995; Rainforth, 1997). Rainforth (1997) noted that the Navajo specimens are poorly preserved and could possibly be distorted *Brasilichnium* tracks.

Ornithischia.—Several specimens attributed to ornithischian dinosaurs have been reported from the Navajo Sandstone of southern Utah. These specimens have been assigned to the ichnogenus *Anomoepus* (Fig. 7C) (Lockley and Hunt, 1995; Rainforth, 1997; Lockley et al., 1998), which has a tetradactyl pes and pentadactyl manus, although digit I of the pes does not always imprint (Olsen and Rainforth, 2003). *Moyenisauripus* is a subjective junior synonym of *Anomoepus* (Olsen and Rainforth, 2003), so Navajo tracks referred to as "*Moyenisauripus*-like" by Lockley et al. (1998) may also be referable to *Anomoepus*. *Otozoum* tracks were not made by an ornithischian dinosaur track-maker (see below) *contra* Lockley and Hunt (1995), Rainforth (1997), and Lockley et al. (1998).

Sauropodomorpha.—Baird (1980) was the first to report "prosauropod" trackways from the Navajo Sandstone. The specimen consists of a single trackway with manus and pes impressions from northern Arizona, which Baird named *Navahopus falcipollex* (Fig. 7D). The pes is tetradactyl and the preserved manus impressions are tridactyl with an enlarged digit I. The offset of manual digit I is a saurischian synapomorphy (Carrano and Wilson, 2001; Yates, 2004) and a manual digit I that is larger than digit II (Fig. 7C) is a character-state that diagnoses the Massospondylidae or a clade within it (depending on the method of character optimization) (Yates, 2004), supporting the referral of *Navahopus* to the Sauropodomorpha. The suggestion that *Navahopus* is synonymous with *Brasilichnium* (e.g., Lockley and Hunt, 1995; Lockley and Meyer, 1999) is unfounded based on the clear morphological differences between the two (Rainforth, 2003).

Tracks referred to *Otozoum moodii* (Fig. 7E) are known from a variety of sites within the Navajo Sandstone of northern Arizona and southern Utah (Lockley and Hunt, 1995; Lockley et al., 1998; Rainforth, 1997; Rainforth, 2003). Pes impressions are pentadactyl with sub-parallel digits II-IV and manus impressions are tetradactyl with no impression of the distal portion of the manual digits (Rainforth, 2003). This ichnotaxon has been assigned to many different tetrapods over the years; many considered it either a basal archosaur (e.g., Baird, 1980) or an ornithischian dinosaur (e.g., Lockley and Hunt, 1995). Rainforth (2003) recently revised *Otozoum*, concluded that *Otozoum* was not synonymous with *Pseudotetrasauropus*, *contra* Lockley and Meyer (1999), and confirmed that the Navajo tracks are referable to *O. moodii*. The results of both quantitative and synapomorphy-based identification studies show that the *Otozoum* trackway maker was a sauropodomorph (Rainforth, 2003). The co-occurrence of *Otozoum* and *Navahopus* suggest the presence of at least two separate morphs of sauropodomorph dinosaurs. Each morph is likely to

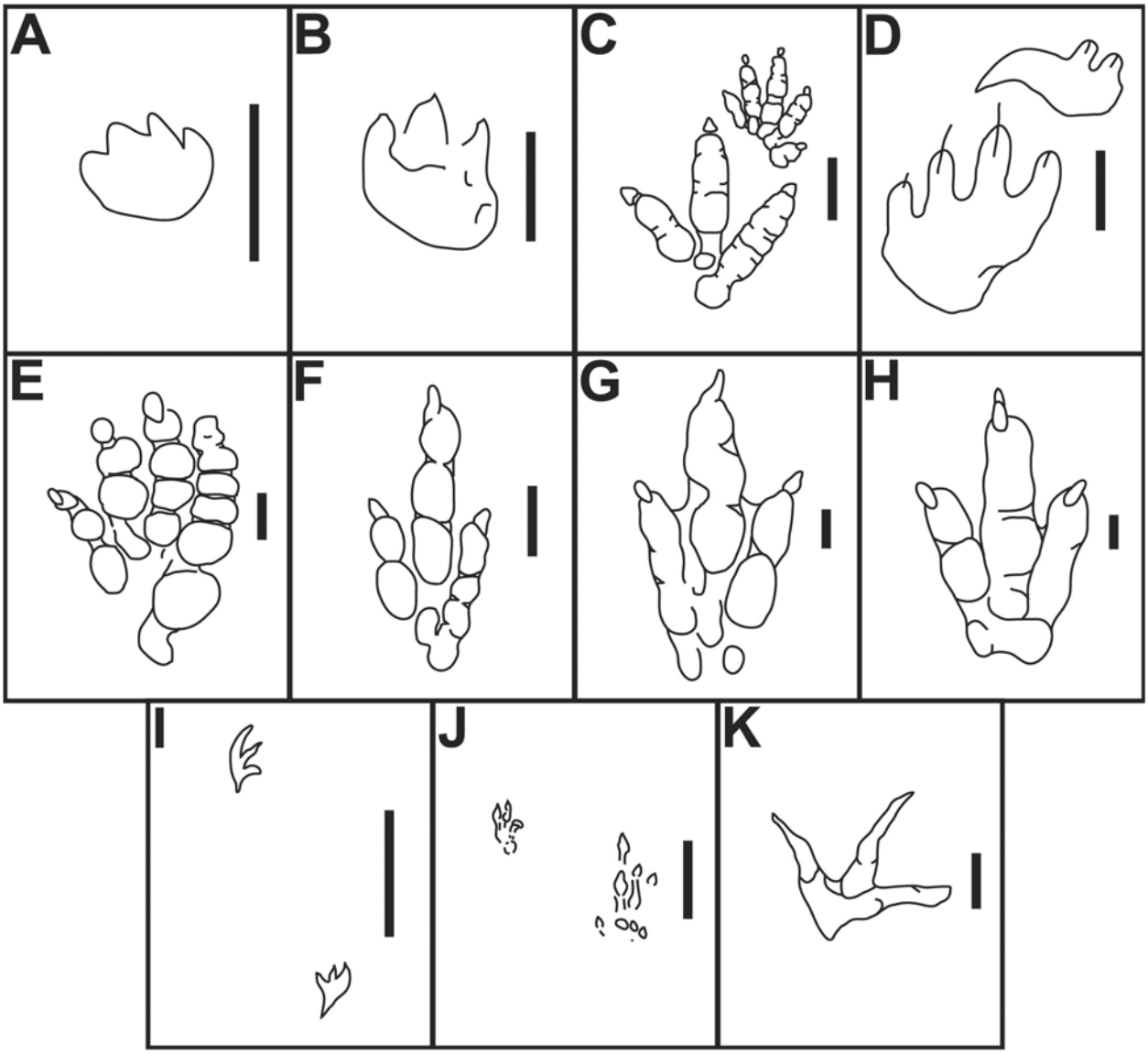

FIGURE 7. Representative vertebrate ichnotaxa from the Navajo Sandstone of northern Arizona and southern Utah. *A*, *Brasilichnium* (redrawn from Rainforth, 1997). *B*, cf. *Batrachopus* (redrawn from Rainforth, 1997). *C*, *Anomoepus* (redrawn from Olsen and Rainforth, 2003). *D*, *Navahopus* (redrawn from Baird, 1980). *E*, *Otozoum* (redrawn from Lockley and Hunt, 1995). *F*, *Grallator* (redrawn from Olsen et al., 1998). *G*, *Anchisauripus* (redrawn from Olsen et al., 1998). *H*, *Eubrontes* (redrawn from Olsen et al., 1998). *I*, cf. *Lacertipus* (redrawn from Lockley and Hunt, 1995). *J*, "lacertilian" (redrawn from Lockley and Hunt, 1995). *K*, *Trisauropodiscus moabensis* (redrawn from Lockley et al., 1992). Scale bar equals 1 cm in *A*; 5 cm in *B*, *C*, *D*, *E*, *H*, *I*, *J*; and 2 cm in *F*, *G*, *K*.

represent several species because vertebrate footprints cannot be referred to specific body-fossil species (Baird, 1980; Carrano and Wilson, 2001).

Theropoda.—Footprints and trackways assigned to theropods are among the most common vertebrate ichnofossils in the Navajo Sandstone of northern Arizona and Utah (Lockley and Hunt, 1995; Lockley et al., 1998; Rainforth, 1997), especially in interdunal facies (Rainforth, 1997). All of the tracks are bipedal with functionally tridactyl pes impressions that have a divarication angle between digits II and IV of less than 45º (Olsen et al., 1998). Traditionally, these footprints have been assigned to one of three Early Mesozoic ichnotaxa, *Grallator* (Fig. 7F), *Anchisauripus* (Fig. 7G), and *Eubrontes* (Fig. 7H), based on size and digit proportions (Olsen et al., 1998). *Grallator*, the smallest, is by far the most common of the three in the Navajo Sandstone (Rainforth, 1997). Although each taxon is clearly diagnosable (Olsen et al., 1998), bivariate plots of pedal digit ratios show that majority of variation of these traits within and among the three taxa can be

described by a single regression function (Olsen, 1980; Olsen et al., 1998). This suggests that *Grallator*, *Anchisauripus*, and *Eubrontes* represent a single growth series of an unidentified clade of theropods (Olsen et al., 1998). Using synapomorphy-based identification methods, these ichnotaxa cannot be identified beyond the clade Theropoda (Olsen et al., 1998).

Ambiguous and problematic footprints. — Tracks from southern Utah variously referred to as *Lacertipus* and cf. *Lacertipus* (Fig. 7I) have been briefly described by Lockley and Hunt (1995). They suggest that it may be the running trackway of the *Brasilichnium* trackmaker; however, this has not been conclusively demonstrated using synapomorphies or other discrete methods. On one slab of *Brasilichnium* and cf. *Lacertipus* tracks from southern Utah, Lockley and Hunt (1995: Fig. 4.21) figure tracks labeled as "lacertilian tracks" (Fig. 7J) that are not mentioned in the text. They were briefly mentioned by Rainforth (1997), but have not been described or properly figured, so it is impossible to say anything about their track morphology or trackmaker.

Lockley et al. (1992) described four footprints from the Navajo Sandstone of southern Utah as a new species of the bird-like ichnotaxon *Trisauropodiscus*, *T. moabensis* (Fig. 7K). *Trisauropodiscus* is a footprint that is tetradactyl with a reversed hallux and a wide divarication angle between digit II and IV. It is known from a variety of early Mesozoic sites in Africa (Lockley et al., 1992). Similar footprints have also been described from the Late Triassic of Argentina (Melchor et al., 2002). The Navajo tracks lack a hallux impression, although this may be a result of the substrate competence. Except for the lack of the hallux, the footprint matches all other criteria for avian footprints set forth by Lockley et al. (1992). As noted by Chiappe (1995), although these footprints are very avian-like, many features influence footprint morphology besides pes morphology, and there are no unambiguous synapomorphies linking *Trisauropodiscus* to Aves. Rainforth (2001b) noted the similarity of *Trisauropodiscus* tracks to *Anomoepus*, and suggested they might be made by an ornithischian. Considering the lengthy temporal gap between *Trisauropodiscus* and the first avian body fossils, the null hypothesis is that these tracks represent non-avian dinosaurs, and this has yet to be falsified in a convincing manner.

Concordance of body fossil and ichnofossil faunas.— Considering the paucity of vertebrate body fossils and richness of vertebrate ichnofossils in the Navajo Sandstone, it is surprising how well the two records correspond. Both are represented by synapsids (Tritylidontidae indet. and *Brasilichnium*), crocodylomorphs (Crocodylomorpha indet. and cf. *Batrachopus*), sauropodomorphs (Plateosauria indet., Sauropodomorpha indet., and *Navahopus* and *Otozoum*), theropods (*Segisaurus* and *Grallator*, *Anchisauripus*, and *Eubrontes*). In the case of the sauropodomorph UCMP 82961 and *Navahopus*, both have synapomorphies that suggest a relationship with the Massospondylidae (*sensu* Yates, 2004). Ichnotaxa that clearly lack body fossil correlates include *Otozoum* and *Trisauropodiscus*, but this is to be expected because of the lack of vertebrate body fossils and the rarity of these ichnotaxa in the Navajo Sandstone. Ambiguous footprint records whose trackmakers are unclear include the "pterosaur", *Lacertipus*, and "lacertilian" tracks.

RELATIONSHIPS WITH OTHER EARLY JURASSIC ASSEMBLAGES

The Navajo vertebrate assemblage, although limited, seems to be typical for Early Jurassic terrestrial assemblages of North America. The Navajo Sandstones shares with other Glen Canyon Group units (Sues et al., 1994) and the McCoy Brook Formation in Nova Scotia (Shubin et al., 1994) a fauna dominated by non-mammalian synapsids, basal crocodylomorphs, basal sauropodomorphs, theropods, and very rare ornithischians. Faunal elements not identified in the Navajo, probably resulting from both taphonomy and paleoecology, include any confirmed records of Chondrichthyes, Osteichthyes, or Sphenodontia (all of which are found in both the Kayenta and McCoy Brook Formations), the diverse basal lissamphibians and turtles of the Kayenta Formation, and any record of basal mammaliaforms such as morganucodontids (Shubin et al., 1991; Sues et al., 1994). All of the ichnotaxa known from the Navajo Sandstone are also known from the Early Jurassic Newark Supergroup of eastern North America, except *Brasilichnium*, *Navahopus*, and *Trisauropodiscus* (Olsen and Padian, 1986; Olsen and Rainforth, 2003; Olsen et al., 1998; Rainforth, 2003). An unusual vertebrate assemblage from northern Mexico may also be Early Jurassic in age, and also has the common tetrapod elements listed above, in addition to a bizarre endemic burrowing lepidosaur (Clark et al., 1994).

Globally, Early Jurassic tetrapod assemblages are remarkably homogeneous (Olsen and Galton, 1977; 1984; Attridge et al., 1985; Shubin et al., 1991; Sues and Reisz, 1995; Irmis, 2004). The continental Lower Jurassic of Britain is biased towards smaller vertebrates, as they are preserved in fissure fills, but does contain numerous tritylodonts similar to those found in the Early Jurassic of western North America

(Sues, 1985; Evans and Kermack, 1994). South African Early Jurassic taxa in common with the Navajo assemblage include basal crocodylomorphs (Gow, 2000; Clark and Sues, 2002), basal sauropodomorphs (e.g., Cooper, 1981), theropods (Olsen and Galton, 1984), and ornithischians (Sereno, 1991; Rainforth, 2003). The Lufeng assemblage of China contains representatives of every clade found in the Navajo Sandstone, as well as sphenodontians and basal mammaliaforms (Luo and Wu, 1994). Thus, the Navajo Sandstone fauna, although limited, lends additional support to the wide distribution of terrestrial tetrapods during the Early Jurassic. Combining the dataset available for the Navajo Sandstone with that of the upper portion of the Newark Supergroup, it appears that the later part of the Early Jurassic did not differ substantially in terrestrial tetrapod faunal composition from earlier Early Jurassic sediments.

CONCLUSIONS

The eolian and associated environments of the Lower Jurassic Navajo Sandstone preserve an important Early Jurassic tetrapod assemblage. Although the body fossil record is limited, when supplemented with abundant footprints, it records a fauna that includes non-mammalian synapsids, crocodylomorphs, ornithischians, basal sauropodomorphs, and basal theropods. The body fossils are preserved in both dune and interdune deposits, probably a result of both paleoecology and taphonomy. Footprints are found in both depositional settings, and corroborate the body fossil record. As a whole, the fauna corresponds well with other North American Early Jurassic assemblages, although it does contain some unique forms of otherwise widely distributed clades (e.g., *Navahopus* and *Segisaurus*). The Navajo assemblage is also broadly comparable with Early Jurassic tetrapod assemblages worldwide, reaffirming the homogeneity of Early Jurassic terrestrial tetrapod assemblages.

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Erratum: The opening in Figure 5 labeled as the obturator foramen is actually the pubic fenestra, and vice versa